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VARIATION IN YUCCA WHIPPLEI

Lee Haines

Yucca Whipplei, a species which is widespread and abundant in southern California, is a member of the family Agavaceae Hutchinson. It ranges from Laguna Seca Chapala in northern Lower California (29° 30′ N. Lat.) to Chew's Ridge in Monterey County, California (36° 30′ N. Lat.). The species varies greatly in appearance and it is apparent from casual observation that the variants are geographical in some degree. However, the nature of the genus *Yucca* is such that this variation can be studied adequately only in the field. Few herbarium specimens exist and these afford at best only the most general information as to the nature of the plant. The investigation has accordingly been carried on solely in the field. This was particularly necessary since it was found from preliminary observations that the size and conformation of the flower and fruit have essentially the same degree of variability throughout the species and that any conclusions must perforce be drawn from a comparative quantitative study of the vegetative characteristics and habit of the inflorescence.

The author acknowledges his indebtedness to the board of graduate research of the University of California, Los Angeles, for funds with which the extended field work was carried on and his gratitude to Dr. Carl Epling, under whose guidance this work was done, to Dr. H. G. MacMillan for help in the preparation of the figures and to many colleagues for assistance in the field.

Distribution

Before any observations or measurements could be made, it was necessary to discover where, in the vast area within its limits, *Yucca Whipplei* grows. The distribution area was divided into geographic sections and reconnoitered in an automobile by traversing as many of the highways, secondary roads, fire roads, and truck-trails as possible. By traveling approximately four thousand miles, the entire area was surveyed and the approximate distribution limits of the species were established (fig. 1). During this reconnaissance, stops were made at favorable localities and observations and measurements were recorded. Such a locality was treated as a field station, designated by a number, and located on a topographic map.

In Lower California the distribution has not been determined in detail. The species was observed at the Laguna Seca Chapala, in the mountains east of Rosario, in the chaparral-covered coastal hills near Sacaton between Ensenada and San Vicente, and north of Ensenada. In southern California it is found in the mountains from Campo northward through the Laguna and Balkan moun-

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tains to the San Jacinto and Santa Ana mountains. It is continuous in a narrow strip from the San Jacinto Mountains to the San Bernardino, San Gabriel, Santa Susana, and Santa Monica mountains to Mount Piños and the Tehachapi mountains. Here the area divides, one branch extending northward in the Piute and Greenhorn mountains and to the western margin of Sequoia National Park, the other passing northward through the Santa Ynez, San Rafael, and Santa Lucia mountains to Chew's Ridge, north of Tassajara Hot Springs in Monterey County. The species is maritime from the Santa Monica Mountains northward. Southward from Walker Pass to the eastern end of the San Bernardino Mountains, it occurs on the margin of the Mojave Desert.

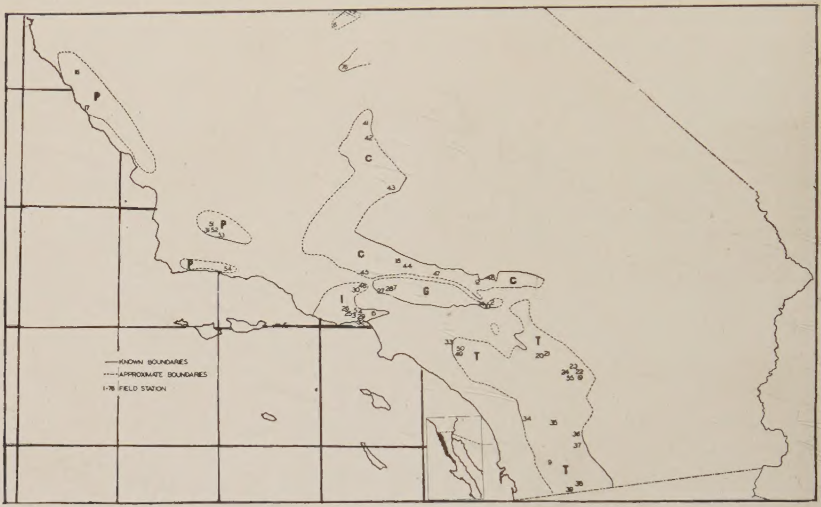

FIG. 1. Distribution of *Yucca Whipplei* in California and Baja California. G, subsp. *Parishii;* P, subsp. *percursa;* I, subsp. *intermedia;* C, subsp. *caespitosa;* T, subsp. *typica.*

The distribution of *Yucca Whipplei* is not continuous throughout its range. There are major gaps between the Santa Ana and the Santa Monica mountains, between the Santa Monica and the Santa Ynez mountains, between the San Rafael and the Santa Lucia mountains, and between the Walker Pass region and the region along the western border of Sequoia National Park. Within these lesser areas the species is either diffuse and general or may be localized. Throughout its entire range *Yucca Whipplei* usually occurs in very porous, shallow soil or on rocky outcrops at elevations from sea level up to 6000 or 8000 feet. When growing on ridges or walls it is found on slopes which have an exposure toward the south.

GROWTH-FORMS

It soon became apparent from field observation that at least four types of growth-forms exist in this species and that these forms are correlated with the geographic distribution. These growth-forms may be briefly characterized as follows: (1) a solitary form, with a simple unbranched, bulbous stem which dies as soon as the plant has flowered; (2) a caespitose form in which the stem branches on the surface of the ground to form a clump of plants composed of from four to one hundred or more distinct rosettes, several of which may send up flower stalks in the same season; in this case, numerous rosettes are formed before any flowering takes place (fig. 2, D); (3) a caespitose form, occasionally solitary, in which the stem branches by means of axillary buds which form short lateral branches; in this case new rosettes are usually formed only after flowering and the dying back of a

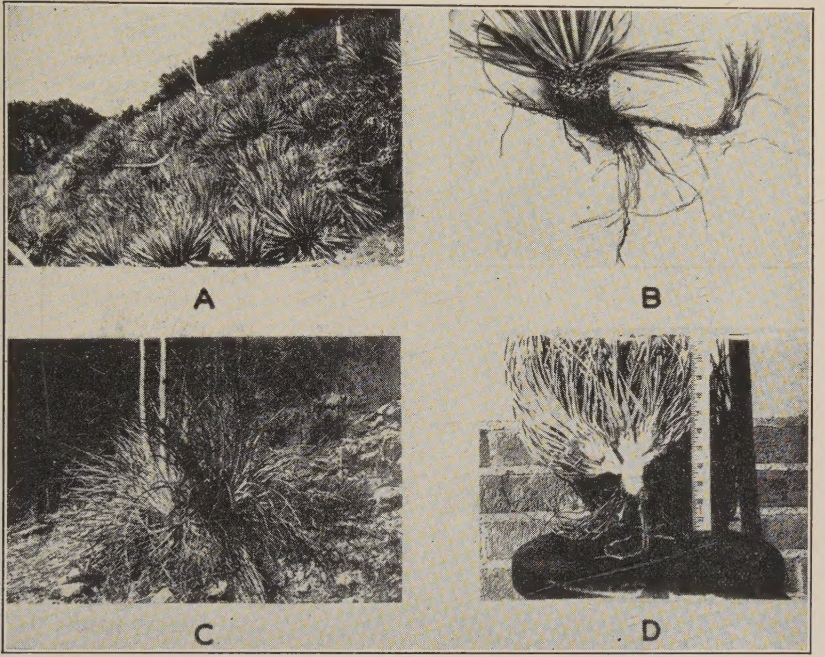

FIG. 2. *Yucca Whipplei.* A, a colony, perhaps a single clone, of subsp. *percursa,* San Rafael Mountains. B, a single plant from such a colony showing a short newly developed rhizome. C, an individual of subsp. *intermedia,* Santa Monica Mountains. The branch on the left has died back after flowering, that on the right has developed from an axillary bud on the dead branch. D, a small specimen of subsp. *caespitosa* from Walker Pass showing the method of branching from the original stem. Such proliferation may continue before flowering takes place until a clump of a hundred or more rosettes is formed.

branch; one or several rosettes may thus be formed, but only one flower stalk is usually produced in any given season (fig. 2, C); and (4) a rhizomatous form, the stem branching by means of underground rhizomes to form dense colonies of asexually produced individuals (fig. 2, A, B).

The solitary form (1) occurs in San Diego, Riverside, Orange, San Bernardino, and Los Angeles counties in two regions which are geographically isolated. They are indicated in Figure 1 by the letters "T" and "G." Actually each of these regions is occupied by a distinct form which may be segregated on the basis of size. The caespitose form (2) with many rosettes, of which several flower in each season, occurs on the western margin of the Mojave Desert from the San Bernardino Mountains east and north to Tehachapi Pass and from there into the Piute and Greenhorn mountains. The distribution of this form is indicated in Figure 1 by the letter "C." The caespitose form with few rosettes (3), only one flowering in each season, occurs throughout the Santa Monica and Santa Susana mountains in the area marked "I." The rhizomatous form (4) occurs in the San Rafael, Santa Ynez and Santa Lucia mountains; its distribution is indicated in Figure 1 by "P". The only point at which any of these races are known to merge and exhibit intermediates lies in the Cajon Pass area where hybridization is apparently frequent between the solitary montane form and the caespitose desert form. There are also two isolated regions in the southern Sierra in which *Yucca Whipplei* grows: along the western border of Sequoia National Park and on the Middle Fork of the Tule River in the Sierra Nevada foothills. The data regarding these two localities are incomplete and the plants growing there (as well as those of Lower California) have been eliminated from present consideration. It seems probable, that although the proportions are similar to those of the solitary form, they are distinct and form another subspecies because of the nature of branching.

Variation of Inflorescence and Leaves

After discovering that the members of this species possessed four forms of growth habit, the question arose as to whether the morphology of the inflorescence and proportions of the whole plant might not be correlated with the growth habit and geographic distribution. The answer to this question is based upon a statistical treatment of the measurements taken at each field station.

The following characters were recorded for each of 1114 plants studied in the field (certain other characters were also recorded, but these were found not significant for the present purposes): (1) the height of the flower stalk, (2) the length of the panicle, (3) diameter of the panicle at its widest point, (4) the diameter of the flower stalk as measured one meter above the surface of the ground, and (5) the length of the leaves. The measurement of characters (1) and (2) were made to the nearest six inches, while character (3) was measured to the nearest inch. At a point one meter above the ground level, the diameter of the flower stalk (4) was measured with outside calipers to the nearest eighth of an inch. The length of the leaf (5) was measured to the nearest inch (fig. 3, C).

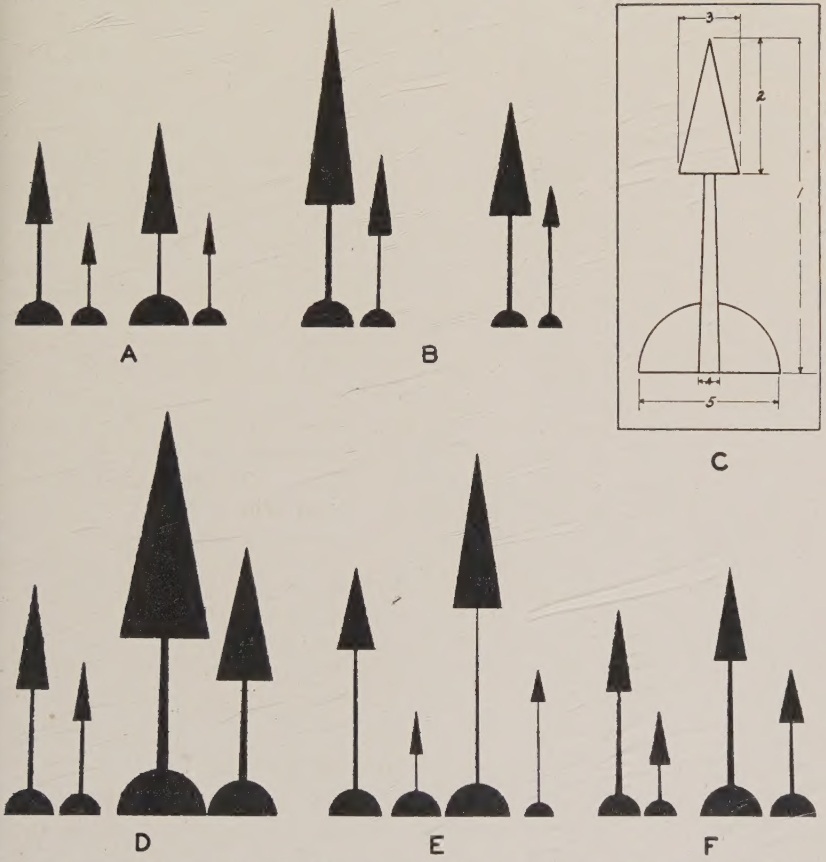

Fig. 3. Ideographs which summarize the measurements made upon twenty plants of *Yucca Whipplei* from ten stations. Each pair of stations is from the same geographic region and was so chosen as to illustrate the extremes of variation measured in that region. A, subsp. *caespitosa;* B, subsp. *percursa;* D, subsp. *Parishii;* E, subsp. *intermedia;* F, subsp. *typica.* The dimensions measured are shown in C. The stations follow: A, left, station 43, eight miles northwest of Mojave, Kern County; A, right, station 47, 1 mile above Valyermo; B, left, station 16, Santa Lucia Memorial Camp, Monterey County; B, right, station 51, 5 miles north of Los Olivos, Santa Barbara County; D, left, Arrowhead Springs, San Bernardino County; D, right, station 28, Tujunga Wash, Los Angeles County; E, left, station 26, Malibu Lake, Los Angeles County; E, right, station 15, West Los Angeles; F, left, station 35, 2 miles south of Lake Henshaw, San Diego County; F, right, station 21, 10 miles east of Hemet, Riverside County.

TABLE 1

Arithmetic Means for Measurements of Morphological Characters of *Yucca Whipplei* from Each Field Station, Showing the Total Range of Variation in the Species

Field Station Number	Number of Plants	Height of Flower Stalk in Feet	Length of Panicle in Feet	Diameter of Panicle in Inches	Diameter of Flower Stalk in Inches	Length of Leaves in Inches
4	16	8.47	3.53	13.80	1.23	21.70
6	14	13.90	6.46	21.70	3.21	34.00
7	12	12.40	5.58	34.20	3.16	29.50
8	12	13.00	6.33	25.10	3.02	28.50
9	17	7.35	2.70	11.10	1.83	25.00
10	19	9.65	4.02	11.70	2.59	25.90
12	12	9.07	4.17	13.30	1.96	22.40
13	12	8.71	3.92	14.90	1.87	21.40
14	12	12.67	6.20	12.67	3.02	31.00
15	48	10.45	3.65	17.35	1.42	28.74
16	24	11.45	5.95	21.60	2.70	24.33
17	24	10.30	4.94	16.60	1.79	25.70
18	36	7.65	3.54	12.10	1.88	21.00
19	16	9.80	4.15	19.00	3.42	25.50
20	12	8.70	3.30	14.50	2.33	32.00
21	12	10.00	4.30	14.75	2.26	28.70
22	25	9.20	3.83	14.80	3.23	21.40
23	12	9.65	4.00	16.20	3.21	24.00
24	12	8.76	4.16	17.40	3.16	24.00
25	48	7.15	2.98	13.40	1.00	24.20
26	52	8.60	3.27	14.10	1.10	26.30
27	12	17.40	9.33	33.90	4.71	29.00
28	12	16.36	8.96	32.40	4.20	32.50
29	53	9.93	3.87	17.30	1.42	28.45
30	36	9.13	3.88	14.80	1.31	25.80
31	36	9.70	5.03	16.03	2.44	16.47
32	13	10.20	3.96	16.05	1.34	30.15
33	12	7.68	2.72	9.35	1.39	25.80
34	12	8.90	3.22	12.60	1.43	29.30
35	24	6.90	2.87	11.10	1.46	20.30
36	12	6.92	3.08	12.67	1.58	21.70
37	12	9.00	4.21	16.40	2.81	26.20
38	12	6.50	2.67	10.20	1.28	21.50
39	12	6.45	2.46	11.20	1.23	21.20
40	24	8.70	3.50	15.50	1.22	33.40
41	26	6.60	2.54	10.00	1.00	20.20
42	24	9.05	3.62	14.20	1.44	25.50
43	36	6.54	2.56	9.75	1.26	22.60
44	12	6.50	2.85	9.60	1.00	18.20
45	12	8.75	3.62	15.30	1.25	29.60
46	12	9.17	4.20	17.85	1.36	29.60
47	25	8.42	3.58	16.95	1.23	18.70
48	25	5.90	2.78	9.16	.86	18.52
49	36	7.90	3.30	10.80	1.57	23.60
50	13	8.48	3.38	12.10	1.56	22.20
51	25	9.18	4.42	15.90	2.09	17.30
52	25	8.88	4.44	16.16	1.89	16.44
53	50	7.91	3.61	13.50	1.62	16.04
54	17	9.60	4.26	15.50	1.88	22.60
76	48	15.10	7.86	23.90	3.64	43.00

In Table 1 are listed the field stations whose locations are indicated by number in Figure 1 together with the number of plants measured at each station and the average value of each of these five characters. The data given in Table 1 show the mean measurements for each station but not the range; that is, the differences between two plants which might be found growing side by side. The ideographs shown in Figure 3 will give an approximate idea of this range, that is, the amount of variation at a given station. The proportions of the individuals, as determined by the measurements indicated, are reconstructed in the ideographs, a method suggested by Edgar Anderson (Ann. Mo. Bot. Gard. 15: 241–332. 1938). Each of the ideographs in Figure 3 represents an individual plant from one of the five geographic regions indicated in Figure 1. The left pair of ideographs in each figure represents the largest and smallest plants found at one station, the right pair of ideographs in each figure, the largest and smallest plants found at a second, but widely separated, station within the same geographic region. These have been selected in such a way as to illustrate the extremes of variation found in each of the five geographical regions.

TABLE 2

Arithmetic Mean, Standard Deviation and Standard Error of the Mean for the Characters Measured and Segregated by Geographic Regions and Growth-Forms

Yucca Whipplei Subspecies	Height of Flower Stalk	Length of Panicle	Diameter of Panicle	Diameter of Flower Stalk	Length of Leaves
caespitosa, C	7.58 ± .102	3.27 ± .587	12.06 ± .247	1.31 ± .028	23.13 ± .340
typica, T	8.32 ± .103	3.14 ± .060	13.30 ± .240	2.14 ± .050	23.93 ± .330
Parishii, G	13.16 ± .369	4.40 ± .253	23.46 ± .942	3.35 ± .109	28.98 ± .637
intermedia, I	9.27 ± .144	3.62 ± .662	15.42 ± .275	1.22 ± .162	26.68 ± .305
percursa, P	9.33 ± .170	4.62 ± .813	16.90 ± .292	1.99 ± .392	18.87 ± .349

The arithmetic mean, the standard deviation and standard error of the mean were computed for each of the five characters of all the plants measured in each geographical region. These data are given in Table 2. From the arithmetic means ideographs were constructed which represent the mean proportions of the inflorescence and leaves of the yuccas of each of the five geographic regions. These are shown in Figure 4, where "G" represents the solitary form growing in the San Bernardino and San Gabriel mountains; "P" represents the rhizomatous form growing in the San Rafael, Santa Ynez and Santa Lucia mountains; "I" represents the caespitose form growing in the Santa Monica and Santa Susana mountains; "T" represents the solitary form growing in San Diego, Riverside and Orange counties; and

"C" represents the caespitose form growing on the western margin of the Mojave Desert.

These ideographs indicate that there is a recognizable difference in the mean morphology of the inflorescence and proportions of the vegetative parts which is correlated with the four forms of growth habit of the stem. This fact is consonant with and gives a quantitative expression of facts which had already been recognized intuitively from more or less casual observation. The differences between the two solitary forms "G" and "T" are so marked that the author proposes to separate them purely on the basis of the size and proportion of the inflorescence, particularly since the two forms are geographically segregated.

In order to determine whether the differences presented in Table 2 and Figure 4, are statistically significant, the standard error of difference was computed for the one hundred possible combinations of comparable characters represented in the ideographs. The resultant differences are recorded in Table 3, and expressed as critical ratios. When the critical ratio has a value greater than three, it is assumed that the differences between the means are statistically significant and that the characters measured may safely be considered as having arisen from sepa-

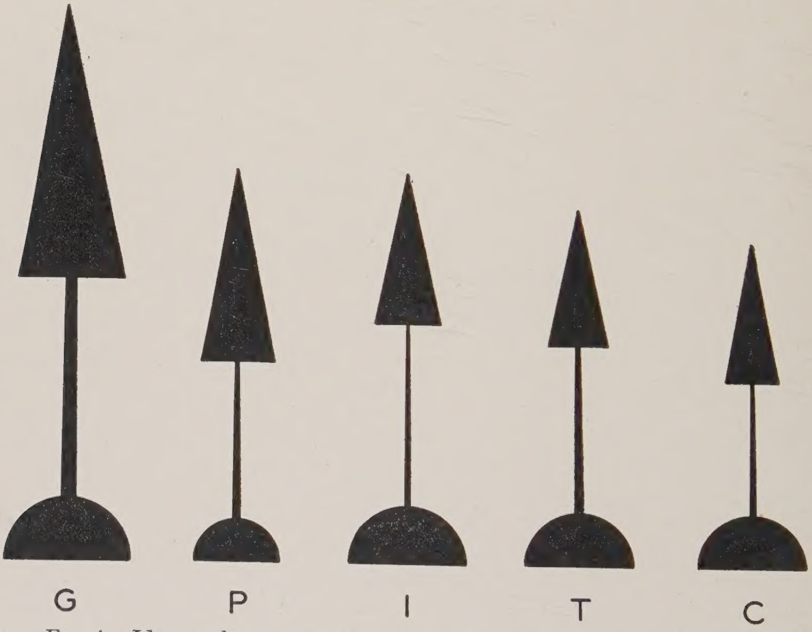

Fig. 4. Ideographs representing the mean proportions of five regional subspecies of *Yucca Whipplei*: G, subsp. *Parishii;* P, subsp. *percursa;* I, subsp. *intermedia;* T, subsp. *typica;* C, subsp. *caespitosa.*

rate populations in which the true values for these characters are not alike.

TABLE 3

Critical Ratios Derived from the Standard Error of Difference between One Hundred Pairs of Means, as Shown

		typica	Parishii	intermedia	percursa	caespitosa
Parishii	h.F.S.		9.83	6.20	5.05	5.10
	l.Pan.		4.83	0.72*	1.81*	0.22*
	d.Pan.		10.45	5.80	9.55	3.58
	d.F.S.		10.10	5.45	0.38*	2.92
	l.Lvs.		7.05	6.13	10.40	1.69*
typica	h.F.S.			10.10	11.90	14.60
	l.Pan.			1.10*	0.25*	1.77*
	d.Pan.			8.20	6.66	11.70
	d.F.S.			10.90	3.34	182.00
	l.Lvs.			3.26	10.11	9.05
intermedia	h.F.S.				0.29*	11.05
	l.Pan.				0.74*	0.39*
	d.Pan.				3.70	9.10
	d.F.S.				1.82*	0.55*
	l.Lvs.				16.80	11.00
percursa	h.F.S.					8.83
	l.Pan.					0.77*
	d.Pan.					12.60
	d.F.S.					1.73*
	l.Lvs.					8.75

* Critical ratios which do not indicate a significant difference between the two means compared.

h.F.S.—height of flower stalk.
l.Pan.—length of panicle.
d.Pan.—diameter of panicle.
d.F.S.—diameter of flower stalk.
l.Lvs.—length of leaves.

While these ratios are statistically significant, their taxonomic significance must be interpreted largely upon the basis of experience. These critical ratios suggest that the order of significance of the morphological characters are: the diameter of the panicle, the height of the flower stalk, the length of the leaves, the diameter of the flower stalk, and the length of the panicle.

While some of the characters compared in Table 3 are not significantly different, the summation of habit which they express is. It is therefore clear that each geographic race or growth-form may be distinguished solely by mean size and proportions of its inflorescence and leaves.

Conclusion

It has been shown above that *Yucca Whipplei* is represented throughout its range by four growth-forms and that significant differences of inflorescence and leaves are correlated with these growth-forms. Furthermore, it has been shown that one growth-form, the solitary type, is characteristic of two forms which differ significantly in habit of inflorescence and foliage and are geographically segregated. It appears, therefore, that *Yucca Whipplei* is represented by not less than five geographic races. That others may exist seems possible, in so far as the author is able to judge from the limited number of observations which were made on the forms of Lower California and the Sierra Nevada. The question arises, then, as to a suitable taxonomic treatment of these forms. It seems preferable, until there is evidence that more than geographic barriers segregate them, to treat the geographic races, discussed above, as subspecies.

TAXONOMY

YUCCA WHIPPLEI Torrey, Botany of the Mexican Boundary 22, 1859, type collected by Schott at San Pasqual, San Diego County, California (Torrey Herb., N. Y. Bot. Gard.). *Y. aloifolia* Torrey in Report Whipple Exped., Botany 147, 1856 (not L.). Type collected in Cajon Pass by the Whipple Expedition; since two subspecies with intermediate hybrids occur here it is uncertain to which form this reference applies. *Hesperoyucca Whipplei* Baker in Kew Bull. p. 8, 1892.

Nearly acaulescent, stem simple or branched; leaves in a basal rosette, 0.125–0.75 inches wide, 1–4 feet long, linear-lanceolate, tipped with a slender spine, fibrous, evergreen, flat to more or less triquetrous, finely striate, their margins serrulate; inflorescence 5–20 feet high; panicle oblong, 1.5–11.5 feet long, 0.5–3 feet in diameter; peduncle 0.5–6 inches thick; perianth segments distinct, nearly equal; filaments clavate, attached to the base of the perianth; capsule short-cylindric, 1.5–2 inches long.

KEY TO THE SUBSPECIES

Stem branched, only the flowering branch dying back after flowering, both dead and living rosettes usually present.
  Stem branching by means of rhizomes, forming dense colonies of asexually produced individuals .... a. subsp. *percursa*
  Stem branching on surface of ground, forming a clump of from 4 to 100 or more rosettes; several inflorescences may arise from a clump of rosettes in a single season .... b. subsp. *caespitosa*
  Stem branching by axillary buds to form short lateral branches; only one inflorescence arises from a group of rosettes in a single season .... c. subsp. *intermedia*
Stem unbranched, solitary, the whole plant dying after flowering.
  Flower stalk 5–13 feet in height, 1–4.5 inches in diameter; panicle 1.5–7 feet in length, .5–2 feet in diameter; San Diego, Riverside and Orange counties and northern Lower California .... d. subsp. *typica*
  Flower stalk 7–20 feet in height, 1.5–6 inches in diameter; panicle 3–11.5 feet in length, 1–3 feet in diameter; San Gabriel and San Bernardino mountains ... e. subsp. *Parishii*

a. Yucca Whipplei subsp. **percursa** subsp. nov. Type collected on Cachuma Mountain in the San Rafael Mountains of Santa Barbara County, California, *A. L. Haines* (deposited in the Herbarium, University of California, Los Angeles).

Caudex longitudine 30–60 cm., in basi rhizomata elongata ferens et ut videtur clonum diffusum faciens; rhizomatibus maturis diametro circiter 2–3 cm., longitudine ad 2 m. et ultra; scapo altitudine ad 5 m. maximam partem circiter 3 m.; scapi in altitudine 1 m. supra humum diametro ad 8 cm., maximam partem 5 cm.; paniculis longitudine ad 3 cm., maximam partem circiter 1.5 m. et diametro in latissima parte ad 70 cm., maximam partem circiter 40 cm.; foliorum longitudine ad 1 m., maximam partem circiter 45 cm.

Stem 1 to 2 feet long, producing rhizomes at its lower end; mature rhizomes 1 inch in diameter, 2–6 or more feet in length producing new individuals from the terminal buds to form a dense stand which may be considered as a clone; height of flower stalk 5–16 feet, average 9.3 feet; diameter of flower stalk at one meter above ground .75–3.5 inches, average 1.9 inches; length of panicle, 2–9.5 feet, average 4.6 feet; diameter of panicle at widest point, 6–28 inches, average, 17 inches; length of leaves, 10–35 inches, average 19 inches.

This subspecies is a component of both the coastal sage and chaparral formations, occurring mostly between 200 and 2000 feet; it is found in the San Rafael, Santa Ynez and Santa Lucia mountains of Santa Barbara and Monterey counties.

b. Yucca Whipplei subsp. **caespitosa** comb. nov. *Y. Whipplei* var. *caespitosa* Jones, Contrib. West. Bot. 15: 59. 1929, apparently based upon plants observed on the desert side of Cajon Pass.

Stem branching above the ground to form a crowded, caespitose clump of four to a hundred or more rosettes, several branches in a single clump often flowering at one time; height of flower stalk 4–13 feet, average 7.5 feet; diameter of flower stalk one meter above the ground, .5–2.75 inches, average 1.3 inches; length of panicle, 1.5–6 feet, average 3.25 feet; diameter of panicle at widest point 4–24 inches, average 12 inches; length of leaves 12–40 inches, average 23 inches.

This subspecies is an associate of the desert woodland, occurring particularly with *Juniperus californica,* usually between 2000 and 4000 feet. It may extend down into the upper limits of the desert shrub formation. It ranges north and west from Arrastre Creek in San Bernardino County along the western border of the Mojave Desert to the region of Walker Pass.

c. Yucca Whipplei subsp. **intermedia** subsp. nov. Type collected at Malibu Lake, Santa Monica Mountains, *A. L. Haines* (deposited in the Herbarium, University of California, Los Angeles).

Caudex a gemmis axillaribus pauciramosus in maturitate solum; scapo florifero saepius solitario altitudine ad 5 m. et ultra, maximam partem circiter 3 m. et diametro in altitudine 1 m. supra humum ad 5 cm., maximam partem circiter 3 cm.; paniculae longitudine ad 2.5 m., maximam partem circiter 1 m. et diametro in latissima parte ad 60 cm., maximam partem circiter 38 cm.; foliorum longitudine ad 1 m. et ultra, maximam partem circiter 60 cm.

Stem branching only by axillary buds after it is well matured; base of stem and roots persistent after flowering to form the subterranean portion of the new plants; only one flower stalk produced in a cluster of rosettes at one time; height of flower stalk 5–15.5 feet, average 9.25 feet; diameter of flower stalk, one meter above the surface of the ground, .5–2 inches, average 1.2 inches; length of panicle .5–7.5 feet, average 3.5 feet; diameter of panicle 6–28 inches, average 15 inches; length of leaves 13–40 inches, average 26 inches.

The type of branching of this subspecies seems to be intermediate between that of subsp. *typica* and subsp. *caespitosa.* It is found throughout the Santa Monica and Santa Susana mountains of Los Angeles and Ventura counties and occurs from sea level up to 2000 feet. It is an associate of the coastal sage and chaparral formations, particularly the chamisal of the latter.

d. YUCCA WHIPPLEI subsp. **typica** nom. nov. *Y. Whipplei* Torr. Bot. Mex. Bound. 22. 1859.

Stem simple, solitary, bulbous, dying when fruit has been formed; height of flower stalk 5–13 feet, average 8 feet; diameter of flower stalk, at height of one meter above the ground, 1–4.5 inches, average 2 inches; length of panicle 1.5–7 feet, average 3 feet; diameter of panicle at widest point 6–27 inches, average 13 inches; length of leaves 13–45 inches, average 24 inches.

This subspecies has a stout inflorescence with a thick, short flower stalk bearing a heavy panicle of compact flowers. It occurs from 1000 to 4000 feet and ranges through the Laguna, Balkan, San Jacinto, and Santa Ana mountains. It is associated chiefly with the chaparral formation, particularly the chamisal, but occasionally extends into the coastal sage and desert shrub formations.

e. YUCCA WHIPPLEI subsp. **Parishii** comb. nov. *Y. Whipplei* var. *Parishii* Jones, Contrib. West. Bot. 15: 59. 1929; type collected above Cajon Pass near San Bernardino (?). *Y. graminifolia* Wood, Proc. Acad. Philad. 20: 167. 1868, based upon plants observed in "the mountains twelve miles east of Los Angeles," perhaps near Monrovia.

Stem simple, solitary, dying when fruit has been formed; height of flower stalk 7–20.5 feet, average 13 feet; diameter of flower stalk, at height of one meter above the ground, 1.5–6 inches, average 3.3 inches; length of panicle 3–11.5 feet, average 6.5 feet; diameter of panicle 1–3 feet, average 2 feet; length of leaves 17–46 inches, average 29 inches.

The largest individuals of *Yucca Whipplei* occur in this subspecies. It is distinguishable from the other solitary form of the species by the size of its inflorescence. In all dimensions measured the inflorescence of subsp. *Parishii* is nearly twice as large as the inflorescence of subsp. *typica.* The subspecies is found on the western slopes of the San Bernardino and San Gabriel mountains where it occurs from 1000 to 8000 feet elevation. At lower elevations it occurs with the chaparral and coastal sage formations, at higher elevations it ranges well into the montane forest.

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CERTAIN NORTH AND SOUTH AMERICAN DISTRIBUTIONS IN SCIRPUS

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Recent studies on collections of the cyperaceous genus *Scirpus* L. obtained in South America by the University of California Botanical Expedition to the Andes has revealed a surprisingly high degree of relationship between the species of this genus in the two hemispheres. Although one species is endemic to the California flora a large number of the species is wide ranging making it necessary to study both near and distant floras to discover their true affinities. The genus has many American species. Nothing approaching a general statement may as yet be given for their distribution. Some range widely, whereas others are very narrowly endemic or occupy discontinuous ranges.

The California flora contains sixteen species of *Scirpus* as follows: *S. microcarpus* Presl, *S. Congdoni* Britton, *S. criniger* Gray, *S. paludosus* A. Nels., *S. robustus* Pursh, *S. fluviatilis* (Torr.) Gray, *S. acutus* Muhl., *S. validus* L., *S. californicus* (C. A. Mey.) Steud., *S. Olneyi* Gray, *S. americanus* Pers., *S. nevadensis* Wats., *S. Clementis* Jones, *S. carinatus* Gray, *S. setaceus* L. and *S. cernuus* Vahl. The species known from Argentina were recently well organized by Barros (1). Without following Barros too closely the following entities may be recognized: *S. deserticola* Phil., *S. giganteus* Kunth, *S. paludosus, S. asper* Presl, *S. cubensis* Poepp. & Kunth, *S. californicus, S. validus, S. Olneyi, S. americanus, S. nevadensis, S. atacamensis* (Phil.) Boeckl., *S. rigidus* Boeckl., *S. macrolepis* Boeckl., *S. cernuus* and *S. inundatis* Poir. *Scirpus Clementis, S. criniger* and *S. Congdoni* are endemic in the North American flora while *S. atacamensis, S. rigidus, S. macrolepis, S. giganteus* and *S. deserticola* are endemic in South America. Nearly fifty per cent of the species comprising these two lists occur both in California and in Argentina. An analysis of the distribution of those species which occur both north and south of the equator should afford some information concerning the interchange of species in general between the hemispheres.

In *Scirpus,* the section *Baeothryon* consists of perennials with spikelets uniformly single, terminal, style 3-fid, and achene smooth, brown. It comprises eight species and one variety, namely *S. hudsonianus* (Michx.) Fern., *S. planifolius* Muhl., *S. Clintonii* Gray, *S. rigidus, S. pumilus* Vahl, *S. Clementis, S. cespitosus* L., *S. cespitosus* var. *callosus* and *S. atacamensis.* Three members of this group have a circumboreal distribution, and the fact that this is an old group is attested by the obvious relationship of two Andean endemics to these northern types. Both *Scirpus cespitosus* var. *callosus* and *S. hudsonianus* are found in North America, Europe and Asia. *Scirpus pumilus* occurs in a few isolated stations in North America, in Europe and has been reported from Tibet (5). The end points of migration down the Rocky Mountains, through the montane regions of Central America and into the Andes, are represented apparently by *S. rigidus* of Peru and Bolivia and *S. atacamensis* of Chile and Argentina.

That *Scirpus planifolius* and *S. Clintonii* are most closely related, within the section *Baeothryon,* to *S. hudsonianus* is shown by their mutual possession of cauline leaves and scabrous triangular culms, and is also strongly indicated by the roughly equiformal areas of their North American distribution. On the same morphological grounds the South American *S. rigidus* is more closely related to these three and less closely allied to its geographical partner *S. atacamensis.* The last species has smooth, terete culms and cauline leaves reduced to mucronate sheaths, conditions which demonstrate its affinity with *S. Clementis* and *S. pumilus.* Acceptance of the latter assumption makes it necessary to postulate one of two possibilities as to their geographic origin: (a) a double migration down the Andes from North America; (b) a continuous range from North to South America for some prototype which has diverged along parallel lines of evolution subsequent to the geographic isolation of some of its parts. In either case the history of the plants undoubtedly dates back to the Pliocene when, coincident with the earliest invasion of South America by holarctic fauna (6, 9), one or more of the species may be assumed to have had its widest distribution. Fernald (4) has pointed out that the present fragmentary distribution of *Scirpus pumilus* is probably a direct result of Pleistocene glaciation.

Various species in other sections of the genus show an interruption of their ranges in the tropics. *Scirpus nevadensis* is found to be an uncommon plant in the western United States and Canada occupying strongly saline soils over a wide area. It is rare in

Argentina where it also appears in strongly saline habitats over a wide area. The species is, however, unreported between northern Argentina and Mono County, California. It may have been a coastal, salt marsh type or perhaps was formerly tolerant of fresh or only slightly saline water. Analogies exist today in *S. paludosus, S. americanus,* and *S. acutus* which grow on the sea margins, on the borders of inland fresh-running streams and lakes and in the saline soils of the Great Basin. The uplift of the Rocky Mountains and the Sierra Nevada initiated the changes which resulted in the disappearance of some of the inland lakes and increased the salinity of others. Gradually, in accompaniment with this change, *S. nevadensis* may have developed an adaptive tolerance toward aridity. The southern members of the species may have passed through a similar history but the members between were faced with a different problem; either they disappeared or gave rise to such closely related species as *S. Olneyi* and *S. americanus.*

Scirpus paludosus, S. validus and *S. Olneyi* are similar to *S. nevadensis* in the interruption of their ranges by a broad belt of the tropics including at least Central America and South America north of the Amazon but they differ in being much more abundant in North America than in South America. There are several possible explanations to account for the existence of this broad hiatus in distribution which is certainly not a reflection of incomplete collections: (a) the species may be spreading from the northern to the southern hemisphere and have not yet had time to occupy all of their potential area; (b) these species may, perhaps, have been more abundant in the past but are becoming depleted in the southern hemisphere due to the impact of changing conditions; (c) greater competition in the southern hemisphere flora may possibly have hindered the spread of these species since they first appeared there; (d) since they are not especially tolerant of tropical conditions a migration through that area may have been accomplished by a few of the more tolerant biotypes. *Scirpus paludosus* and *S. validus* are evidently plastic species to which the first alternative may be applicable but *S. Olneyi* appears to be a more rigid type and the other alternatives may have to be called into account.

Scirpus cubensis which is common in Chile is reported also from Panama by Standley (10). *Scirpus inundatus,* known from as far south in Chile as the Valdivian Lakes region is also reported from Costa Rica by Clarke (3, p. 460). *Scirpus cernuus,* a ubiquitous species with a world wide distribution in temperate regions avoids the tropics.

Scirpus californicus and *S. americanus* also have a disrupted range but differ from the preceding species in being widespread and fairly common in both hemispheres. They come nearest to bridging the tropical barrier. *Scirpus californicus* is known from the San Francisco Bay region south to Guatemala, and from Colombia, Ecuador and Brazil to middle latitudes in South America. To this is added *S. californicus* var. **tereticulmis** (Steud.) comb. nov. (*S. tereticulmis* Steud. Syn. Pl. Cyp. 85. 1855) extending the total range from central South America to the Straits of Magellan. A more uniform climate would undoubtedly amplify this broad latitudinal range. There is geological evidence (2) that uniform, moist climates existed at several different periods of Tertiary time.

Scirpus americanus, finally, is known from Nova Scotia and Alberta south to Mexico and from Peru and Brazil to Patagonia. Morphologically similar plants grow indiscriminately in fresh and strongly saline waters. The extreme variability in this species is suggested by the number of taxonomic variations which have been recognized in it. Such a high degree of polymorphy would seem to mark it as a comparatively young species which is reaching the peak of its distribution at the present time.

There has now been presented a graded series of geographical distributions from the endemics of section *Baeothryon* on the one extreme to the ubiquitous *Scirpus americanus* on the other. The most widely ranging species in the series are those with the greatest variation. This fact suggests that at the time when its number of biotypes and range of tolerance is greatest it is possible for a species to cross well-marked climatic barriers. Probably *S. Clementis* and *S. atacamensis* together represent an old species which, with advancing age, depauperization of biotypes and wide separation, became modified in descent to slightly different end points. Since they occupy areas isolated from other members of their section this assumption seems more reasonable than to suppose that they never had a sufficient wealth of biotypes to create an overlapping of their now discrete ranges; that is, chance dispersal or fortuitous origin depend on close relatives living in nearly adjacent territories. The species whose distributional pattern is intermediate in character between those of *S. Clementis* and *S. americanus* may be classed logically as intermediate in age if they no longer occupy their maximum range, or as young species if they have yet to reach a maximum range.

The methods of dispersal of *Scirpus* are not yet completely analyzed. Most species are stoloniferous perennials which migrate easily either up or down stream along muddy river banks. Birds eat the fruits and may carry them for short distances, that is, from one drainage area to another, in their digestive tracts, or in mud adhering to their feet. Undoubtedly important also is the buoyant nature of the fruits, although this is an extremely variable factor. Achenes of *S. americanus* are considered to be non-buoyant but are abundant in lake drift (7) while those of *S. maritimus* L. may float for a month (8, p. 239), not sinking until the pericarp decays. Finally the element of chance dispersal undoubtedly plays a considerable role over a long period of time. The prevalent uniformity of the aquatic habitat must be largely responsible for the high degree of relationship over wide areas.

A conclusion similar to that reached by Matthew (6) in connection with a study of the evolution of land vertebrates may be drawn. It would seem to be unnecessary to postulate any profound change in the existing distribution of land masses to account for the present distribution of *Scirpus* between the two hemispheres. To assume change in climate is probably unnecessary since species are apparently being interchanged between North and South America at the present time, but a more uniform climate would facilitate this process. Such changes as did occur in the past certainly have had their effect on the history of the species concerned, but, apparently, any theory involving cataclysmic phenomena is not essential to account for the migrations of North and South American species of this genus.

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THE PROBLEM OF LIFE ZONES ON MOUNT SHASTA, CALIFORNIA

William Bridge Cooke

In 1898 a party led by Dr. C. Hart Merriam made a biological survey of Mount Shasta. In the report (6) published in 1899 Dr. Merriam defined the several life zones he found on the mountain on the basis of his earlier discussion of North American life and crop zones (5). The writer, after four years of study, has come to the conclusion that two of the three zones must be revised or clarified (or, as to one of them, completely eliminated) in order that the casual visitor and future worker may be less confused as to the boundaries of the upper zones. The present paper is an attempt to point out some of the problems encountered and the conclusions resulting from a study of these problems.

The Upper Sonoran zone (in Merriam's terminology) occurs within sight of the mountain in Shasta Valley to the north, in Sacramento Valley to the south, and in the valleys of the Great Basin areas to the east, for example, the areas found in the vicinity of the Modoc Lava Beds National Monument (1). On Mount Shasta this zone does not occur above 4000 feet, the contour line which has been chosen as the lower limit of the area covered by this study.

The Transition zone is clearly differentiated on Mount Shasta. Where the base of the mountain extends down to 4000 feet this zone can be divided into two minor belts. The lower of these may be called the Chaparral Belt. The term refers here to a Transition zone chaparral, a broader interpretation than that of Cooper (2). Wherever the Transition zone forest has been disturbed on the mountain a dense growth of chaparral has taken its place and to a certain extent has invaded the remaining forested portions. Before the Shasta National Forest was established, great areas of timber were logged. Fire contributed to the further destruction of whatever forest might have been left so that the former forest composition must be reconstructed by study of the accounts of early travelers and from isolated trees and small groves throughout the area. The zone is dominated by *Arctostaphylos patula* and *Ceanothus velutinus.* Additional shrubs include: *Ceanothus cordulatus, C. divaricatus, C. prostratus, Castanopsis sempervirens, C. chrysophylla, Purshia tridentata, Pachystima myrsinites* and others listed in Table 1.

Above the chaparral belt there is a narrow belt of forest, typical of the normal Sierran Transition zone except that on the northeast quarter of the mountain there occurs a large stand of *Pinus contorta* var. *Murrayana* which almost completely replaces the normal forest association. The normal forest, except where it is invaded by the chaparral, includes the following coniferous species: *Pinus ponderosa, P. Lambertiana, P. monticola, P. attenuata, P. contorta* var. *Murrayana, Abies concolor, A. magnifica* var. *shastensis, Libocedrus decurrens* and *Pseudotsuga taxifolia.* Various species of deciduous trees and shrubs which form lower stories in this forest are listed in Table 1.

Above the Transition zone forest is the Canadian zone as interpreted by Merriam. Except on the northeast side it is almost wholly composed of *Abies magnifica* var. *shastensis* which covers an altitudinal belt of from 500 to 1500 feet around the mountain. At the head of Panther Creek, and between the east side of Gray Butte and the west side of Mud Creek Canyon, and at one or two other small isolated stations, *Tsuga Mertensiana* enters this forest. Locally there may be colonies of from a few hemlocks in the fir forest to a few firs in the hemlock forest. In the vicinity of upper

TABLE 1

Species of woody plants occurring in the Transition Chaparral (Ch), Transition Forest (T), Canadian (Ca) and Hudsonian (H) zones on Mount Shasta, compared with the Zone Indicators of Hall and Grinnell (3) for Upper Sonoran (US), Transition (T), Canadian (Ca) and Hudsonian (H) zones.

Species	Position on Shasta	Zone Indicator
Abies concolor	ChTCa	T
Abies magnifica var. shastensis	TCaH	Ca
Acer glabrum	TCa	Ca
Alnus viridis var. sinuata	CaH	
Amelanchier alnifolia	ChT	
Arctostaphylos nevadensis	TCaH	Ca
Arctostaphylos patula	ChTCa	T
Castanopsis chrysophylla	ChT	T
Castanopsis sempervirens	ChTCaH	Ca
Ceanothus cordulatus	Ch	
Ceanothus divaricatus	Ch	US
Ceanothus prostratus	ChT	T
Ceanothus velutinus	ChTCa	T
Cercocarpus ledifolius	CaH	
Chamaebatiaria millefolium	Ca	
Chrysothamnus Bloomeri var. angustatus	ChTCaH	
Chrysothamnus nauseosus var. occidentalis	Ch	
Cornus californica	T	
Cornus Nuttallii	Ch	T
Juniperus communis var. montana	H	
Kalmia polifolia	CaH	H
Libocedrus decurrens	ChT	T
Lutkea pectinata	CaH	
Pachystima myrsinites	Ch	
Phyllodoce empetriformis	CaH	
Pinus albicaulis	CaH	H
Pinus attenuata	ChT	US
Pinus contorta var. Murrayana	TCa	Ca
Pinus Lambertiana	ChT	T
Pinus monticola	TCa	Ca
Pinus ponderosa	ChT	T
Pinus ponderosa var. Jeffreyi	TCa	Ca
Populus tremuloides	TH	Ca
Populus trichocarpa	T	
Prunus demisa	Ch	T
Prunus emarginata	ChTCa	
Prunus subcordata	Ch	
Pseudotsuga taxifolia	ChT	T
Purshia tridentata	ChT	US
Ribes cereum	ChTCaH	
Ribes divaricatum	Ch	
Ribes nevadense	T	
Ribes Roezlii	ChTCa	
Ribes viscosissimum	ChTCa	
Salix Scouleriana	ChTCa	
Sambucus caerulea	ChT	
Sambucus racemosa	Ca	
Tsuga Mertensiana	CaH	H
Vaccinium caespitosum	Ca	
Vaccinium occidentale	TCa	Ca

TABLE 2

Species of herbs occurring in the Canadian (Ca), Hudsonian (H), and Subalpine (A) zones on Mount Shasta compared with zonal distribution of previous records (Arctic-Alpine, AA), and with the Hall and Grinnell Indicator lists.

Species	Position on Shasta	Reported position	Indicator of Zone
Achillea lanulosa var. alpicola	H	AA	
Carex Breweri	CaHA	AA	AA
Carex phaeocephala	A		
Dicentra uniflora	CaH	AA	
Draba Breweri	HA	AA	AA
Erigeron compositus var. trifidus	HA	AA	H
Hulsea nana	HA	AA	AA
Juncus Parryi	CaHA	AA	
Lewisia pygmaea	H		AA
Lewisia triphylla	H	AA	Ca
Oxyria digyna	CaHA	AA	AA
Penstemon Menziesii var. Davidsonii	CaHA	HAA	AA
Phacelia frigida	HA	AA	
Poa Pringlei	A		
Polemonium shastense	HA	AA	
Polygonum minimum	H		
Polygonum Parryi	H		
Polygonum shastense	CaHA	HA	H
Potentilla flabellifolia	H	H	Ca
Potentilla Sibbaldii	H	H	AA
Saxifraga Tolmiei	HA	AA	AA
Silene Watsonii	HA	AA	

Squaw Valley Creek hemlock makes up nearly seventy-five per cent of the forest cover. In the middle and lower portions of the zone a few individuals of *Pinus monticola* may be scattered among the firs. However, along the west bank of Mud Creek Canyon this species is represented by scattered individuals from the upper limit of erect firs to the middle of the Transition zone forest. One of the interesting features of this zone is the forest on the northeast quarter where the Canadian zone may not exist at all, or where it may be considered as replacing the Transition zone forest. Here species of the Transition zone, including *Pinus ponderosa* (possibly the variety *Jeffreyi*) and *Abies concolor* mingle in a mixed forest with (a) species from the Hudsonian zone, including *Pinus albicaulis* and *Juniperus communis* var. *montana;* (b) species from the Canadian zone, including *Abies magnifica* var. *shastensis* and *Pinus monticola;* and (c) the anomalous species (at least on Mount Shasta) *Pinus contorta* var. *Murrayana, Castanopsis sempervirens* and *Ribes cereum.*

At the borders of the Canadian zone are broad areas transitional to the Hudsonian zone above and the Transition zone below. The belt on the lower side includes *Abies concolor, A. magnifica* var. *shastensis* and *Pinus ponderosa* var. *Jeffreyi.* In a swamp at Wagon Camp *Vaccinium occidentale* is dominant. The belt on the upper side includes semierect or dwarfed specimens of *Pinus albicaulis, Abies magnifica* var. *shastensis* and *Tsuga Mertensiana.* These transitional belts could be labeled with the combined names of their commoner species: "Mixed Fir-Jeffrey Pine belt" and "Pine-Fir-Hemlock belt." In addition to the coniferous trees which have been mentioned as components of the Canadian zone, a number of broadleaf trees and shrubs occur in the area. In the dry forests are *Ribes cereum, R. viscosissimum, Cercocarpus ledifolius* and *Populus tremuloides;* while in the meadows and spring areas occur *Phyllodoce empetriformis, Kalmia polifolia, Lutkea pectinata* and *Alnus viridis* var. *sinuata* in addition to others listed in Table 1. Arms of the previously mentioned chaparral extend into this zone.

It is above the Canadian zone that difficulties are encountered. These difficulties lie in the interpretation of timberline, in the distinction between the Canadian and Hudsonian zones and in the presence or absence of an Arctic-Alpine zone.

Merriam considered an Arctic-Alpine zone present on the mountain. He thought that timberline coincided with the highest limits of *Pinus albicaulis,* even though at its highest limits all individuals are reduced to mats of from a few inches to a foot or more in height. With this interpretation, timberline is the upper limit of the Hudsonian zone, which is almost exclusively made up of, and is characterized by, *Pinus albicaulis.* Timberline, then, according to Merriam, divides the Arctic-Alpine from the Hudsonian zone. Thus timberline extends up most ridges on the mountain to heights of from 9000 to 9500 feet, with occasional arms up to 10,000 feet. The basins formed by Post-Pleistocene glacial cirques, and by moraine materials at about 8000 to 8500 feet would have a much lower timberline, perhaps between 8000 and 8500 feet, depending on the more or less strict application of the term to isolated stands of pines on the faces of minor ridges (with barren gulleys between and below them) and to the presence or absence of trees of any height on the flats below these ridges. The Arctic-Alpine zone, then, would include the areas on ridges on which a fair stand of dwarf pine occurs and which lie in the shade most of the day and thus are considerably cooler in climate. These cooler ridge slopes are on the south and east sides of the ridges and hold snow banks longer, at a lower elevation, than other more exposed areas. In one place, at least, on the north side of Red Butte, there is a small timberline area with a growth of plants above it. This small community was included by Merriam in the Arctic-Alpine zone because of its more severe climate as indicated by an association of plants which includes: *Polemonium shastense, Silene Watsonii, Oxyria digyna, Saxifraga Tolmiei* and others. However, it was admitted that on top of the Butte, several hundred feet above this colony, there is a fairly large stand of Hudsonian zone timber. A number of similar "Arctic-Alpine" associations occur below timberline as conceived by Merriam, some of which grow in climatically restricted areas such as this, while others occur in apparently normal Hudsonian zone climate.

There are other conceptions of what constitutes timberline. We are referring here, of course, to alpine timberline rather than to sea-level poleward timberline, or to those desert or grassland associations on the borders of which tree species drop out in transition belts. United States forest rangers of the Shasta National Forest consider timberline as the upper altitudinal limit of upright tree growth. This is an economic interpretation of the word. In this sense the line or belt between the Canadian and Hudsonian zones is timberline. According to Hopkins (4, 7): "Climatic timberline may be defined as the poleward sea-level or alpine altitude limit of upright growth of tree species, under otherwise favorable conditions, as distinguished from dwarf or prostrate forms of the same species, as controlled by the climatic elements of temperature, wind, snow, ice, etc.; and also as distinguished from limits of tree growth due to the absence of suitable soil, moisture, or the presence of local glaciers." In the sense of Hopkins, then, Merriam's Shasta Hudsonian zone would occur above climatic timberline (which coincides with the economic timberline of the forest ranger).

Proceeding to the problem of the Merriam Arctic-Alpine zone on Mount Shasta, it should be noted that the term "Arctic-Alpine" is misleading. Conditions of growth in the arctic circle are different from those in an alpine habitat where the air pressure is lower, the proportion of daylight nearly the same as that normal to the latitude under consideration and temperature change during the growing season more frequent. Since these factors affect food production and other physiological processes of the vegetation the Arctic zone should be differentiated from the Alpine. On Mount Shasta, then, the vegetation may be considered alpine rather than arctic and according to either Merriam or Hopkins the zone would occur above the limits of tree growth. This zone, therefore, if recognized on Mount Shasta, is characterized purely by herbaceous plants.

The Alpine zone may be interpreted in terms of associations or an association of plants, in which sense Merriam occasionally used the term in discussing the flora of the mountain. On Mount Shasta a number of species reputedly occur (6) above tree-line. These include: *Polemonium shastense, Oxyria digyna, Phacelia frigida, Silene Watsonii, Draba Breweri, Carex Breweri, Juncus Parryi, Dicentra uniflora, Saxifraga Tolmiei* and others. However, all these species have been discovered below the upper limits of tree growth in various habitats such as draws, flats, gulleys and ridges which occur in Merriam's Hudsonian zone; all these species have been observed in association with *Pinus albicaulis*. The only species yet known which occur above timberline as delimited by Merriam and not also below it are *Carex phaeocephala* and *Poa Pringlei* both of which were collected in 1939 along the Summit Trail in an area which Merriam would have called truly alpine since it lies at between 9000 and 10,000 feet, in the cirque in question fully 500 to 1000 feet above the highest limits of his interpretation of timberline. Merriam had no temperature records upon which to base his Shasta Alpine zone. He therefore based it upon the association of plants found in an area which should have certain theoretical temperatures. But is this association truly alpine when all but two of its constituents (these two unreported until recently) are found in the Hudsonian zone?

Hopkins defines the bioclimatic zones in three major zones and a number of minor zones. The three major zones include: I. "North and south, polar or arctic and alpine, humid or arid major regions of the Frigid Zone." II. "North and South, temperate or intermediate latitudes or altitudes, major arid and humid regions of the Temperate Zone." III. "Tropical and equatorial low and high land, humid and arid major regions of the tropical zone." Four groups of minor zones, of which group 4 is warmest, are described under Major zone I. Upper minor zone 4 is defined as "Arctic and alpine above and below perpetual ice and snow, lower transition or snow line zone." Under Major zone II, Hopkins describes seven groups of minor zones of which group "1" pertains to the present problem. Under "Upper minor zone 1" the following definition is listed: "High latitudes and altitudes, subarctic and alpine regions and areas above climatic timberline or its equivalent, 'timberline zone.'" "Lower minor zone 1" is "timberline."

Mount Shasta has no permanent snow line. The five glaciers which are still active are confined to areas above 10,000 feet and apparently have no immediate effect on the surrounding vegetation. In their vicinity the soil is too poor and the drainage too complete for an association of plants to survive even though no glacier occurred. The permanent snow fields on the mountain are small and scattered and have little effect on the minimal vegetation in their vicinity largely because they are above the areas where plant life, except lichens and algae, survives even sparsely.

From these considerations, an Alpine zone on Mount Shasta is not to be expected. Certainly if permanent snow lines do not exist on the mountain, by definition, Major zone I is absent. The next zone is Major zone II, Upper minor 1. This is subalpine, and from areas of greater distribution of plants, might even be considered upper Hudsonian. However, the finer threads cannot be split until more definite statistics are available for the climate of the mountain, especially in its upper regions, throughout the year.

Foster, Warren County, Ohio,
December, 1939.

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A NEW SPECIES OF LOTUS FROM THE MOUNT HAMILTON RANGE, CALIFORNIA

HELEN K. SHARSMITH

Lotus rubriflorus sp. nov. Herba annua albosericea, pilis longis; caules 1–5 aliquando decumbentes, 3–10 cm. longi; folia 10–16 mm. longa exstipulata, 4-foliolata imparipinnata, rachibus complanatis, foliolis lanceolatis acutis, 2–11 mm. longis; flores solitarii axillares subsessiles, 6–7 mm. longi; calyx dense pilosus lobis linearibus acuminatis, 4–5 mm. longis, corollam aequantibus; petala rubra in aetate caerulescentia; legumina pilosa oblonga dehiscentia, 8–9 mm. longa.

Slender annual; stems 1–5 (mostly 2–4) from base, 3–10 (mostly 4–8) cm. long, usually somewhat decumbent; herbage pilose throughout with long, white, silky, somewhat appressed or spreading hairs; leaves 10–16 mm. long, exstipulate, imparipinnate; rachis flattened, about 1 mm. broad; leaflets 4, two appearing terminal, the remaining two on one side of the rachis, 2–11 mm. long, subsessile, lanceolate, acute, terminal leaflets often slightly falcate; flowers 6–7 mm. long, solitary, axillary, subsessile, usually bracteate; calyx 6–7 mm. long, densely pilose; tube 1.5–2 mm. long; lobes linear, acuminate, 4–5 mm. long, equalling corolla; petals glabrous, clear bright pinkish red (aster purple[1]), fading bluish, claws white, banner 5 mm. long; wings shorter than or about equalling keel, posterior dorsal lobes large and very narrowly margined with white; keel 5 mm. long, apex somewhat pointed, body very narrowly margined with white dorsally and posteriorly; ovary densely pilose, dorsal margin straight, ventral margin curved; style pilose below, glabrous above, curved near base; legumes pilose, 8–9 mm. long, 2.5 mm. wide, oblong, stramineous; seeds 2–4, 2 mm. long, 2 mm. wide, irregularly lens

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[1] Ridgway, R. Color standards and color nomenclature, plate 12. 1912.

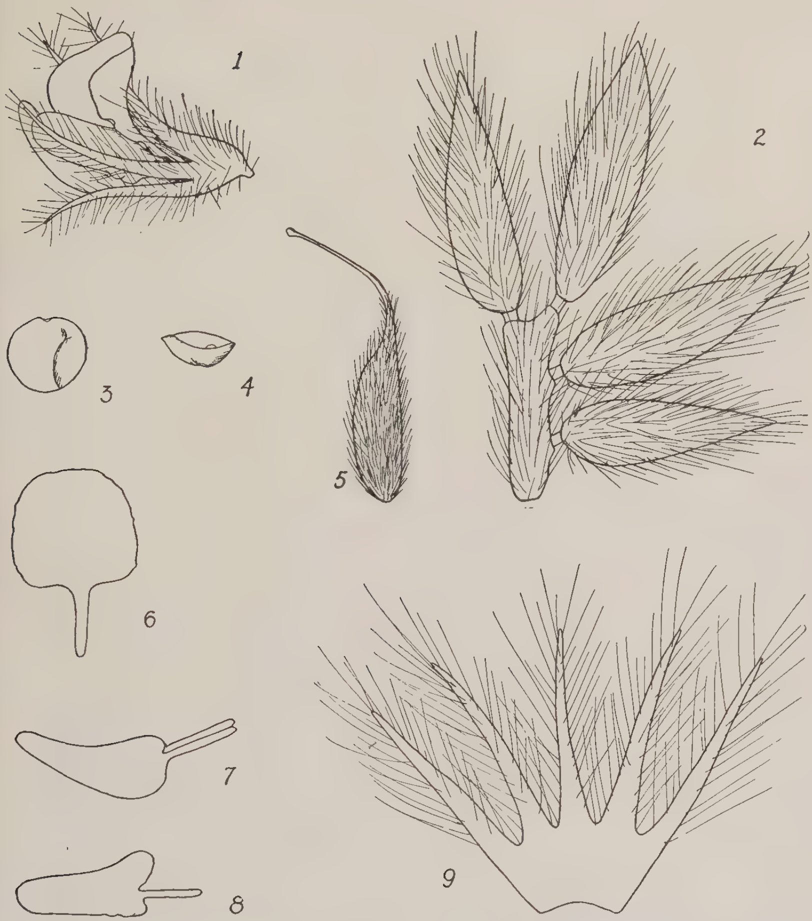

Fig. 1. *Lotus rubriflorus* H. K. Sharsmith: *1,* flower; *2,* leaf; *3,* seed, lateral view; *4,* seed, anterior view showing hilum; *5,* ovary; *6,* banner; *7,* keel; *8,* wing; *9,* interior of calyx. All × 5.

shaped, angled, notched at hilum, olive green to light brown, usually mottled with deeper brown, the surface often with a bronze sheen.

Type. Rolling hills at north end of Adobe Valley, Stanislaus County, Mount Hamilton Range, California, altitude 1600 feet, April 22, 1936, *A. M. Carter & H. K. Sharsmith 3544,* in flower (Herb. Univ. Calif. No. 605765; isotypes, Gray Herb., U. S. Nat. Herb., Mo. Bot. Gard., Stanford, Kew). Topotype. June 5, 1938, *A. M. Carter & J. L. Morrison 1403,* in fruit (Herb. Univ. Calif.; duplicate topotypes deposited with isotypes).

Lotus rubriflorus has been found only at the type locality, but within the one known colony the plants are abundant. Collections made two years apart suggest that the species is not merely transient at this locality. It inhabits sparse grassland in an open stand of *Quercus Douglasii,* growing in association with the common vernal annuals of the region, such as *Lotus subpinnatus, L. humistratus, Orthocarpus attenuatus, Microseris linearifolia, M. sylvatica, Pentachaeta exilis, Plagiobothrys canescens.*

On the basis of the pinnate, short, exstipulate leaves, the small, solitary flowers, and the straight, beakless, dehiscent legumes, *Lotus rubriflorus* belongs to the subgenus *Acmispon* (Raf.) Ottley (Univ. Calif. Publ. Bot. 10: 197. 1923). Within this subgenus, *L. rubriflorus* is most closely associated with *L. denticulatus* Greene, *L. subpinnatus* Lag., and *L. humistratus* Greene, these species all having dilated leaf rachises, few, inequilateral leaflets, subsessile flowers, and flattened, angled seeds.

Although growing in association with *Lotus humistratus* and *L. subpinnatus, L. rubriflorus* is a very distinct, easily recognized species. It most closely resembles *L. humistratus* in pubescence, length of calyx lobes, and shape and size of legumes, but is more pilose, and the calyx lobes are longer. It differs strikingly from *L. humistratus,* as well as from *L. denticulatus* and *L. subpinnatus,* in the lanceolate leaflets. Furthermore, the flower color of *Lotus rubriflorus* is exceptional; in North American representatives of the genus the corolla is characteristically whitish or yellow, although often veined, streaked or suffused with red, pink, or purple, or may fade red. In *L. rubriflorus* the corolla is a uniform red. The following key brings out these distinguishing features and separates *L. rubriflorus* from those species to which it is most nearly related:

Leaflets obovate, often obtuse; flowers cream color to yellow, tinged with or fading red or purple	*L. denticulatus* *L. humistratus* *L. subpinnatus*
Leaflets lanceolate, acute; flowers bright pinkish red, fading bluish	*L. rubriflorus*

State College of Washington,
Pullman, Washington,
February, 1939.

REVIEWS

A Monograph of the Genus Calochortus. By Marion Ownbey. Annals of the Missouri Botanical Garden. Volume XXVII. Pp. 371–560. St. Louis, December 10, 1940.

The genus *Calochortus,* ranging from Nebraska to the Pacific and from Guatemala to British Columbia, is treated by Dr. Ownbey in three sections, *Eucalochortus, Mariposa* and *Cyclobothra.*

The sections are divided into twelve subsections under which are arranged the fifty-seven species and thirteen varieties.

Dr. Ownbey's approach to the problems in *Calochortus* from the viewpoint of herbarium study, extensive field work, garden cultures and cytological investigation gives his work a definitiveness possessed by too few monographs. While some botanists may feel that he has admitted to specific rank several entities that might better have received subspecific status, on the whole his decisions seem to be based on a firm foundation of evidence both from comparative morphology and from geographic distribution.

The publication of seven new species and ten new varieties should arouse keen interest in the further study of local areas. Of great significance in this connection is the speciation that has taken place in the Siskiyou Mountains of southern Oregon and northern California where four local, very distinct, rarely collected species are found. This area should continue to be a fertile collecting ground.

Because of the cytogenetic approach and the fact that Dr. Ownbey is now working in the west where garden cultures and field studies may be carried on we await with great interest any additional developments in the phylogenetic analysis of this genus.—JOHN L. MORRISON, Department of Botany, University of California, Berkeley.

The Flora of Whatcom County, State of Washington. By W. C. MUENSCHER. Pp. 1–134, with 10 figures and 1 table. William A. Church Company, Ithaca, New York, 1941. Published by the author.

A county flora is so rarely prepared for a portion of any of the western states that the appearance of a less excellent volume than the present one evokes especial comment.

The twenty-three hundred square miles comprising Whatcom County occupy the northernmost county of the Pacific Coast and extend in altitude from near sea-level on Puget Sound to 10,750 feet at the summit of Mount Baker, one of the principal peaks of the Cascade Range. With the coastal hills in the Transition life zone, and timberline on Mount Baker at only 6000 feet, all of the boreal zones are thus represented in a relatively small altitudinal range as well as in a small area. With these facts in mind, one will be less astonished at the inclusion of 1042 species and varieties. The author contributed an earlier catalogue of the same area to "Muhlenbergia" in 1914, and has noted additions to this original list, chiefly in "Torreya" and MADROÑO, during the subsequent years. A substantial portion of the list is owing to the writer's predilection for aquatic and introduced plants, both of which are too likely to be overlooked by collectors. Although the plant records of the present book are based primarily upon Dr. Muenscher's own collections, the first set of which is preserved in the herbarium of Cornell University, he has consulted the collections of others as well.

The diversity of topics treated in the introduction reflects the author's wide botanical interests. An interesting feature is the presentation of lists of those species characteristic of such distinctive habitats as alpine meadows, salt marshes, gravelly prairies and coastal cliffs. A brief account of the zonation of vegetation is handsomely illustrated by carefully selected photographs. A conveniently classified list is offered of plants deemed suitable for cultivation.

In the annotated catalogue, which constitutes two-thirds of the book, the genera and species are alphabetically arranged under the systematically ordered families. Neither keys nor descriptions are provided. The abundance and characteristic habitats of each species are described and authenticating specimens are cited for each. It thus becomes possible for the perennially skeptical specialist to check the identity of every item attributed to the group with which he is especially concerned.

The taxonomic treatment is, on the whole, conservative, and pretty thoroughly up to date. The current bitter controversy between the advocates of "subspecies" and the proponents of "varieties" is met by calling all subspecific entities, except forms, "varieties," and retaining the original authors of the trinomials, regardless of whether they designated the subspecific or varietal category. This has the curious effect of attributing "varieties" to such authors as Hall and Clements, Piper, and Pennell, which will probably bring down the wrath of both factions. There is also some inconsistency in the capitalization of specific names, which will doubtless provide ammunition for the arsenal of those advocating uniform decapitalization.

This flora is, happily, much more than an unusually complete and attractively prepared catalogue of the plants of one western county. Because of the wide range of habitats and altitudes contained in this one political division, it is essentially a catalogue of the flora of western Washington. It is to be hoped that the completion of this very satisfactory study will encourage the preparation of other much needed local floras throughout the west.—L. Constance, Department of Botany, University of California, Berkeley.

Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants. By Jens Clausen, David D. Keck and William M. Hiesey. Carnegie Institution of Washington publication 520. Pp. vii + 452. 1940. Paper, $3.50. Bound, $4.50.

This stimulating volume represents the application of methods in experimental taxonomy to an understanding of the involved intrarelationship of several complicated groups of species. The application of the method to specific problems serves in this case as a vehicle to outline the method of research. The groups of plants selected are *Potentilla glandulosa* and its allies, *P. gracilis* and its allies, *P. Drummondii* and *P. Breweri, Horkelia fusca* and *H. californica,* the genus *Zauschneria,* certain groups of *Penstemon,* the *Achillea millefolium* complex, the *Artemisia vulgaris* complex and a large number of well selected minor problems in groups ranging from the Gramineae through the Compositae. The volume is prefaced with a short historical sketch of the research project; a brief tribute is paid to the late Dr. Harvey Monroe Hall under whose able direction the work was begun. It is a point of major interest that the authorship should include a cytogeneticist, a taxonomist and a plant physiologist.

In establishing the experimental method the problem was approached from many points of view and several methods were tried and discarded before the final procedure was adopted. The plant materials selected were those that could be used as clone transplants. A clone is defined by the authors as "all asexual propagules derived from one individual." These were subjected to varied environments: cytogenetic studies were made: a revised taxonomic analysis was presented based upon the results of these experiments. The terminology follows closely that of Turesson.

For purposes of review the treatment of *Potentilla glandulosa* and its allies (section *Drymocallis*) affords an illustration of the mode of attack. This group had received varied and haphazard treatment at the hands of the old school taxonomists. It was selected because of its widespread vertical and horizontal distribution, its great variability and its ready adaptability to garden manipulation. Specifically, California ecotypes from the following stations were used: Coast Range; Sierra Nevada, foothill, mid-altitude meadow, subalpine and alpine. These differed morphologically and showed some variability in seasonal rhythm. They possessed the uniform chromosome number $n = 7$. There are no genetic barriers between them. Clone transplants of each ecotype were established in California at three stations: a coastal station at Stanford University, a middle station at Mather, and a timberline station near Saddlebag Lake. The latter stations are in the Sierra Nevada.

Observations were made to determine constant characters, seasonal differences, effects of light and moisture differences and effects of altitude. The reversibility of environmental modifications was established for some ecotypes by taking clone members of changed individuals back to the original environment.

In general it was found that each ecotype retained a certain individuality in all three stations. This was regarded as being due to the sum total of hereditary characters. Each responded to the different environments in a very characteristic way; these changes (modifications) were superimposed over the hereditary characters. While morphological change was slight the annual cycle or response to the rhythm of seasonal events was profoundly changed. In some cases, however, this change was not sufficient to insure survival.

Cytogenetic studies had as their objective "to interpret the taxonomic status of the various forms by testing the degrees of genetic relationship, to explore their evolutionary background by analysis of gene or chromosome differences and to determine their utility for various ecogenetic investigations." In determining whether they were dealing with ecospecies or ecotypes the following criteria were adopted: Crosses between ecotypes would produce a second generation in which the parental genes would be recombined in all proportions without resulting in constitutional weakness of the offspring. In crosses between ecospecies the genic recombinations would produce many constitutionally weak offspring which would barely survive under favorable conditions. Thus there would be constitutional weakness plus environmental unfitness in the offspring of the cross between ecospecies. It has been established in such species of the section *Drymocallis* as have been studied that the "diversity distinguishing ecotypes and ecospecies has been produced by a simple genic differentiation." Genic incompatability, they report, is slight. It was found that hybrids between the ecotypes were easily produced and fully fertile and the conclusion was drawn that they were true ecotypes of a large and variable ecospecies. The authors conclude that "*Potentilla glandulosa* presents a picture of evolutionary differentiation into ecologic units, the ecotypes, which are not separated from each other by breeding barriers. The ecotypes fit their specific climates and differ by many characters, both physical and morphological. Each of these characters appears to be determined by a series of genes, and is often genetically linked with others. The many differences in genes with minute effect furnish the basis for the multiplicity of intergrading forms observed in nature, and the linkage relations suggest a reason for the limited number of taxonomic units that can be recognized in spite of recombinations and lack of internal barriers."

As a result of many such experimental studies certain general conclusions are drawn relative to the problems of regional differentiation. These are discussed in the form of eleven laws governing the nature of modification, its genetic limitations and environmental control and the bearing of modification and genetic differentiation on the development of regional races. Regional races are interpreted as ecotypes or ecospecies which have developed in harmony with their environment through genic differentiation of one sort or another and are under the control of natural selection. Regional differentiation implies discrimination between unlike environments. These units, the ecotype and the ecospecies, are regarded as the natural units of ecological and evolutionary behavior. These conclusions are in close agreement with Turesson's statements regarding the genotypical response of the plant species to its habitat.

The volume is replete with tables and graphs giving comparative measurements of the plant and its parts as it developed in the different environments. Photographic illustrations of plants and of specimen vouchers provide convincing demonstration of the results obtained.

This work at once becomes a classic in the field of experimental taxonomy. Regardless of agreement or disagreement as to precise limitation in the definition of species the problem of the pattern of relationship within closely allied groups is clearly set forth by such methods as these. Obviously it will be impossible to subject all plant groups to similar experimentation. It is hoped, however, that enough such work can be done to complete the picture of the nature of relationships in plants so that a pattern can be established into which such plants as are not adaptable to this mode of treatment can be placed.—HERBERT L. MASON.

NOTES AND NEWS

The following monographic studies and other important taxonomic articles have appeared recently: "preliminary list of desmids of the Pacific Northwest with descriptions of some new forms," by Gordon D. Alcorn (Occas. Papers, Dept. Biol. Coll. Puget Sound, no. 10, 1–200, pls. 1–8. 1940); "the North American sub-divisions of Ranunculus," by Lyman Benson (Amer. Journ. Bot. 27: 799–807, 17 figs. 1940); "a revision of Laurentia and allied genera in North America," by Rogers McVaugh (Bull. Torr. Bot. Club 67: 778–798. 1940); "new combinations and new names in the Umbelliferae," by Mildred Mathias and Lincoln Constance (Bull. Torr. Bot. Club 68: 121–124. 1941); "a revision of Choisya," by Cornelius G. Muller (Amer. Midland Nat. 24: 729–742, 7 figs. 1940); "the American species of Hippocrateaceae," by A. C. Smith (Brittonia 3: 341–355, 12 figs. 1940); "a revision of the genus Chaenactis," by Palmer Stockwell (Contrib. Dudley Herb. 3: 89–168, pls. 22–45. 1940).

Recent articles of general interest to botanists are: "late Tertiary floras of the Great Basin and border area," by Daniel I. Axelrod (Bull. Torr. Bot. Club 67: 477–487. 1940); "some features of the structure of Toxicodendron diversilobum," Herbert F. Copeland and Bernice E. Doyel (Amer. Journ. Bot. 27: 932–939. 1940); "history of botanical exploration in Alaska and Yukon territories from the time of their discovery to 1940," by Eric Hultén (Botaniska Notizer 1940: 289–346. 1940); "Arizona localities of interest to botanists," compiled by T. H. Kearney (mimeographed, received 1941); "additional nomina generica conservanda: Pteridophyta and Phanerogamae," by T. A. Sprague (Kew Bull. Misc. Inf. no. 3: 81–134. 1940); "Gramineae of Nevada," by Jason R. Swallen (Contributions toward a flora of Nevada, no. 1, mimeographed, Washington, D. C.).—ETHEL CRUM.

PROCEEDINGS OF THE CALIFORNIA BOTANICAL SOCIETY

October 24, 1940. Meeting, 2093 Life Sciences Building, University of California, Berkeley, at 7 : 45 P. M. The President, Dr. Ira L. Wiggins, occupied the chair. Dr. Wilfred W. Robbins, Professor of Botany and Botanist in the Experiment Station, University of California, Davis, spoke on, "Alien Plants Growing without Cultivation in California."

November 14, 1940. Meeting, 2093 Life Sciences Building, University of California, Berkeley, at 7 : 45 P. M. The President, Dr. Ira L. Wiggins, occupied the chair. A nominating committee was appointed by the President, to submit nominations for officers of the Society for 1941, and asked to report at the December meeting. Mr. J. W. Stacey, of San Francisco, spoke on, "Distribution and Evolution of the Genus Carex in Western North America."

December 12, 1940. Meeting, 2093 Life Sciences Building, University of California, Berkeley, at 7 : 45 P. M. The President, Dr. Ira L. Wiggins, occupied the chair. Mr. William M. Hiesey, Carnegie Institution of Washington, Stanford University, California, spoke on, "Relations between Plants and Climates as Revealed by Transplant Experiments."

January 16, 1941. Meeting, 2093 Life Sciences Building, University of California, Berkeley, at 7 : 45 P. M. The President, Dr. Ira L. Wiggins, occupied the chair. Miss Ethel K. Crum, Chairman of the Nominating Committee, submitted the names of the following candidates: President, Professor E. B. Babcock; First Vice-President, Mrs. Roxana S. Ferris; Second Vice-President, Dr. Palmer Stockwell; Secretary, Dr. Lincoln Constance; Treasurer, Mr. William M. Hiesey. A motion, made and seconded to accept the report of the nominating committee, was passed unanimously. There were no nominations from the floor. Dr. G. Ledyard Stebbins, Jr., Associate Professor of Genetics, University of California, Berkeley, spoke on, "The Genetic Approach to Problems of Rare and Endemic Species."

February 20, 1941. Meeting, 2093 Life Sciences Building, University of California, Berkeley, at 7 : 45 P. M. The President, Professor E. B. Babcock, occupied the chair. Dr. Ralph W. Chaney, Chairman of the Department of Paleontology, University of California, Berkeley, gave an illustrated lecture on, "Tropical America, a Botancial Garden of the Past."—L. Constance, Secretary.